

DELAYED VOCAL MATURATION IN POLYGYNOUS YELLOW-RUMPED CACIQUES

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ABSTRACT.—Almost all songbird males develop fully crystallized songs before or during their first potential breeding season, when they use these important signals during interactions that determine their social success. We describe a rare phenomenon, in which vocal maturation is delayed until the second potential breeding season, or third year of life, in Yellow-rumped Caciques (*Cacicus cela vitellinus*) from lowland Panama. We heard predefinitive males in their second year sing only uncrystallized song, while three definitive males known to be in their third year sang fully developed songs matching the local dialect. The unusual system of polygynous breeding colonies in caciques may account for why vocal development is delayed. We would expect to find other examples of delayed vocal maturation in polygynous, nonterritorial species, in which second-year males have little opportunity for social success. Received 25 July 2001, accepted 1 July 2002.

Delayed vocal maturation, which we define as the failure of a songbird to develop crystallized song before or during the first potential breeding season, is a rare phenomenon not previously reported in the literature. Song acquisition in songbirds occurs in two phases: a memorization phase, in which acoustic information is stored in the brain after exposure to conspecific song, and a crystallization phase, during which songs are practiced and refined using auditory feedback to compare song output with signals stored in the neural pathways (Konishi 1965, Nottebohm 1999). Memorization of the first songs usually occurs within a few months of hatching, but in some species continues into the first breeding season (Kroodsma 1982, Nelson et al. 1995, Slater and Jones 1995, Waling et al. 1998, Nordby et al. 2001). Other birds continue to acquire new songs or to modify existing ones beyond the yearling period, which may result in increased repertoire size (Nottebohm and Nottebohm 1978, Mountjoy and Lemon 1995), adoption of new local dialect variants (Payne 1985, Trainer 1989), or refining an existing song (O’Loughlen and Rothstein 1993). Studies generally have revealed little variation in the timing of song crystallization. Nearly all songbird species develop their first fully crystallized songs shortly before or sometime during the initial breeding season after hatching (Kroodsma 1982). This timing ensures that males have vocal signals needed to attract

mates, defend territories, or advertise social status. The existence of birds that pass the first breeding season without this important social signal requires explanation. Here we describe delayed vocal maturation in Yellow-rumped Caciques (*Cacicus cela vitellinus*) based on observations of color-banded birds in the field, and discuss reasons why it evolved in light of the unique natural history of this species.

Yellow-rumped Caciques build their hanging nests in tight clusters of 20–100 nests in colonies consisting of one or two trees. Males gather in the nest tree to sing, frequently supplanting one another, and occasionally chasing others out of the tree (Trainer 1988). Colony residents share dialects of 5–7 song types that differ from those at other colonies. Members of a colony exhibit a great deal of uniformity in their renditions of shared song types. The maintenance of this uniformity appears to have great social significance; despite rapid change in the structure of each song type throughout the breeding season, song uniformity persists because each member of a colony adopts the changes. Furthermore, when breeding males disperse between colonies from one breeding season to the next, they adopt the local song types and drop their previous repertoires (Trainer 1989). During bouts of countersinging, males match each other’s song types, which probably helps maintain the linear dominance hierarchy (Trainer 1988).

Dominant males monopolize preferred singing sites nearest the nests, and are most successful at forming sequential consortships with 1–27 females. Males guard their consorts, following them between the nest tree

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TABLE 1. Hatching-year and second-year Yellow-rumped Cacique (*Cacicus cela vitellinus*) males had shorter wings^a and lower body mass^b than after-second-year males. Data are from Panama, January to May, 1981–1983.

| | Wing chord | | | Body mass | | |
|-------------------------------------|------------|------|----------|-----------|------|----------|
| | \bar{x} | SD | <i>n</i> | \bar{x} | SD | <i>n</i> |
| After-second-year males | 174.87 | 4.30 | 23 | 120.84 | 6.72 | 19 |
| Hatching-year and second-year males | 155.06 | 7.39 | 17 | 111.65 | 8.25 | 17 |

^a $t = 9.88, P < 0.005$.

^b $t = 3.64, P < 0.005$.

and the surrounding forest, where females forage or gather nest material (Robinson 1986). Males do not contribute to nest building or rearing young in this system of female defense polygyny. Males acquire the definitive black and yellow plumage by their third year. Second-year (SY) males have a distinct plumage, with darker eyes and olive edges on the contour feathers (Jaramillo and Burke 1999).

METHODS

We conducted our study at one breeding colony in the lowland forest near the Pacific entrance to the Panama Canal (8° 54' N, 79° 34' W) from January to May, 1981–1983. We captured caciques in mist nets suspended from 10-m aluminum poles and banded them with colored PVC bands and a numbered, monel metal band. We recorded body weight, wing chord, and cloacal protuberance of each male captured, and aged individuals on the basis of plumage and eye color. Our analysis of vocal behavior of SY males is based on 360 h of observation of breeding activity at one colony from 16 February to 15 April 1983. We observed 32 occurrences of singing, each lasting 15–45 min, performed by 20 different SY males. SY males, hatched during the previous breeding season, January to May 1982, were 9–15 months old. Males of other songbird species generally have crystallized song by these ages. To compare the behavior of SY males with after-second-year (ASY) males, we noted supplanting, chasing, and grappling among males, and courtship and copulation with females. We recorded songs using a Marantz PMD 340 cassette recorder and an Uher M517 cardioid microphone, and made sonograms using a Kay Elemetrics Model 5500 Sound Spectrum Analyzer with a grey scale video printer.

RESULTS

We found no overlap in the sizes of pre-definitive and definitive males; hatching-year and SY cacique males had significantly shorter wing chords and lower body weight than ASY males (Table 1). Furthermore, the first three outer primary feathers of SY males lacked the notched, tapered ends characteristic

of definitive males. SY males failed to produce the noisy wing beats that ASY males sometimes produce just before landing in the nest tree as part of a flight display. Only 3 of 17 (18%) SY males captured had cloacal protuberances greater than 5 mm, whereas 22 of 23 (96%) of ASY males did.

In the nest tree, SY males generally sat quietly, moved around looking into nests, or chased females as they left the nest tree. When threatened by an ASY male, they adopted a subordinate posture with wings drooping and tail flared. During 78 encounters between SY and ASY males, the older birds always supplanted the younger birds. On a few occasions when an SY male began to vocalize in the nest tree, he was immediately chased from the tree by an ASY male. We did not see any copulations involving SY males, although sightings of matings by ASY males also were infrequent in the study area. Sometimes an SY male performed the precopulatory display toward another SY male, but never toward a female. This display is a seemingly robotic series of head-up poses alternating with tapping the yellow rump patch of the recipient.

Despite constant singing activity by ASY males during daily observation periods, we heard bouts of singing by SY males only 32 times. These bouts occurred only in the forest adjacent to the nest tree, and were either undirected or directed toward a female when she entered the forest. SY males sang only bouts of uncrystallized songs. These bouts differed from those of ASY males in that they were softer, contained numerous incomplete songs, contained unique renditions that occurred only once and did not match any of about 50 song types recorded within 8 km of the nest colony, contained songs that matched local song types but were variable in structure when repeated,

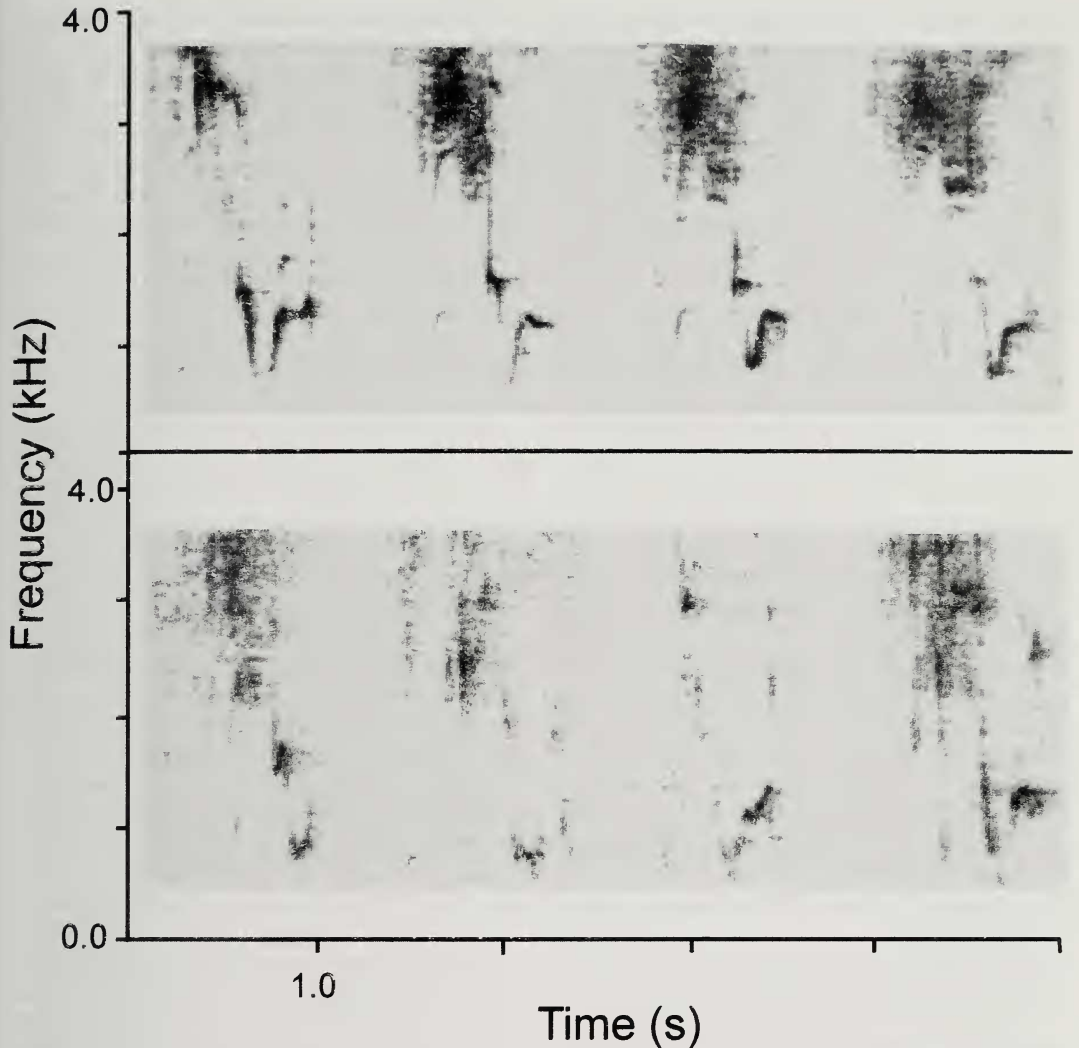


FIG. 1. (Top) The same crystallized song type sung by four Yellow-rumped Caciques in definitive plumage were stereotyped within males and differed little among males. (Bottom) The same song type varied among four uncrystallized renditions sung by one second-year male, and differed structurally from the songs of definitive males. All songs were recorded at the same colony in Panama on 17 April 1983 by J. M. Trainer. Sonograms were made with a Kay Elemetrics Model 5500 Sound Spectrum Analyzer.

and contained song types from more than one colony (Fig. 1). In contrast, ASY males sang only loud bouts in which they repeated stereotyped renditions of song types from only one colony. Three color-banded males, known to be third-year males because they were banded the previous year in predefinitive plumage, sang fully crystallized song.

DISCUSSION

These observations led us to conclude that fully crystallized song matching the local di-

alect appears by the third year in Yellow-rumped Cacique males when they are 21–27 months old. During their second year, or the first potential breeding season, they sing infrequently and then only uncrystallized songs. Hence, song maturation in caciques coincides with acquisition of the definitive plumage. Because we did not examine gonads or measure hormone levels of male caciques, we do not know the relationship between sexual maturity and vocal development. In some songbirds,

increasing steroid hormone levels during the first spring after hatching cause songs to crystallize (Marler et al. 1988, Whaling et al. 1998). Perhaps male caciques do not experience sufficient testosterone levels for song crystallization until their third year.

These findings contrast with numerous songbird species in which crystallized songs develop in time for the first potential breeding season. Even among dozens of species in which SY males have a predefinitive plumage, males are sexually mature, exhibiting normal courtship and singing behavior (Rohwer et al. 1980). Predefinitive SY males of both monogamous and polygynous species sometimes are successful at acquiring territories and mates (Rohwer et al. 1980, Payne 1982). As long as there is some chance of establishing a territory or attracting a mate, it may benefit males to develop crystallized song, even if they retain predefinitive plumage (Studd and Robertson 1985).

However, Yellow-rumped Caciques have an unusual natural history that may account for occurrence of delayed vocal maturation. We propose four factors that explain this rare phenomenon in caciques. First, SY males have almost no chance for reproductive or competitive success. Our observations in Panama and Robinson's (1986) observations of caciques in Peru indicate that the low dominance status of SY males prevents them from monopolizing singing perches, forming consortships or copulating. Because competitive interactions among males occur in breeding aggregations, reproductive interference may make it nearly impossible for young males to reproduce successfully. Selander (1972) similarly argued that delayed plumage maturation is favored by natural selection when young males have a reduced probability of reproductive success. Like caciques, many songbirds with predefinitive plumages are polygynous (Rohwer et al. 1980). The unlikelihood of breeding mitigates the cost of spending the second year with a less effective social signal, be it predefinitive plumage or uncrystallized song.

Second, failure to sing crystallized song in caciques may signal low social status, inviting less aggression and more tolerance from adult males. Similar hypotheses have been proposed for the advantage of having a dull, predefinitive plumage. Males in such plumages may

resemble females or juveniles (Rohwer et al. 1980, Lawton and Lawton 1986), or signal low social status (Lyon and Montgomerie 1986), resulting in less aggression from older males. Unlike many plumage signals, however, song can be switched off in order to avoid an aggressive encounter. Young males with crystallized songs can avoid aggression simply by remaining silent in the presence of a dominant individual. The avoidance of aggression may help explain why SY cacique males avoid singing crystallized song, but additional factors are needed to explain why they fail to develop crystallized song.

Third, were males to develop crystallized songs during their second year, their songs would be socially inappropriate when they later began to breed. Unlike adults, SY males moved among colonies frequently during a breeding season, often appearing at several colonies during a period of a few days (Trainer 1989). Sixty-seven percent of SY males appeared in a different colony the following year when they began to compete for mates. Furthermore, 78% of song types at a colony were different from those present the previous year. Therefore, most SY males are exposed to songs different from the ones they eventually sing when they begin to breed. Given the importance of song conformity within a colony, there would be no advantage for SY males to develop crystallized song.

Fourth, cacique song serves no other social function that would make it beneficial for SY males to sing. For example young cooperatively breeding birds sometimes help defend group territories (Brown 1987). These young birds would be expected to develop crystallized song even though they may have little opportunity to breed.

Delayed vocal maturation is rare among songbirds probably because most birds have an opportunity to learn socially appropriate song before or during their second year, young territorial birds may have a small chance to breed in marginal habitat, and song production can be curtailed to avoid aggression.

Studies of vocal development in bellbirds have revealed interesting parallels with delayed vocal maturation in Yellow-rumped Caciques. D. E. Kroodsmma (pers. comm.) believes that the songs of Three-wattled Bellbirds (*Procnias tricarunculata*) are learned, in

contrast to other suboscines in which song development has been investigated (Kroodsma 1984, 1985, 1989; Kroodsma and Konishi 1991). He observed predefinitive male bellbirds in a contact zone between two song dialects singing two distinct song variants, and recorded change over time in bellbird songs within a locality. These observations are not expected in species with innate song. Based on field observations of three bellbird species aged by plumage appearance (Bearded Bellbird, *Procnias averano*; White Bellbird, *P. alba*; and Three-wattled Bellbird), it appears that the second year of life is pivotal for song development (Snow 1970, 1973, 1977). During this year, males first begin to produce parrot-like squawks only slightly resembling the adult songs. They continue to produce these squawks for several months. Even by the end of the second year, the songs are distinguishable from adult songs as less ringing, shorter, irregular, or incomplete. More recently, D. E. Kroodsma (pers. comm.) has confirmed these findings with observations of color-banded Three-wattled Bellbirds of known age. However, it is unknown to what extent delayed vocal maturation in bellbirds parallels delayed song crystallization in caciques, since the timing of song learning in suboscines in general is not well understood.

Bellbirds breed in dispersed lek territories where males mate polygynously with females. During the breeding season, SY males sing or lurk silently near the boundaries of established territories, but do not possess their own (Snow 1977). Although mating success in bellbirds has not been measured, we speculate that, like young Yellow-rumped Caciques, predefinitive bellbirds may have almost no chance of obtaining a display territory or attracting a female.

Delayed maturation of song in Yellow-rumped Caciques and bellbirds differs from an example of delayed vocal development described for Brown-headed Cowbirds (*Molothrus ater*; O'Loughlen and Rothstein 1993). SY cowbirds from the Sierra Nevada Mountains had crystallized perch songs and flight whistles, but continued to modify their song repertoires until their third year. SY males used their songs to court females, albeit less successfully than adult males in this population (Rothstein et al. 1986). Prolonged song ac-

quisition into the third year may allow cowbirds at high altitudes or latitudes, where the breeding seasons are short and opportunities for exposure to conspecific song limited, to add shared, local song types to their repertoires (O'Loughlen 1995, O'Loughlen and Rothstein 2002).

Delayed vocal maturation has not been reported in three other highly polygynous icterid species, Boat-tailed Grackles (*Quiscalus major*; Poston et al. 1999), Great-tailed Grackles (*Q. mexicanus*; Johnson et al. 2000), and Montezuma Oropendolas (*Psarocolius montezuma*; Webster 1995) although details of vocal development and its timing likewise have not been reported. These species lack distinct, predefinitive plumages, and SY males were not always aged. Furthermore, genetic and behavioral evidence has shown that subordinate males attained some mating success by employing alternative mating strategies (Webster 1995, Poston et al. 1999, Johnson et al. 2000). It is not clear to what extent SY male caciques can take advantage of these alternative strategies.

While delayed vocal maturation is rare, further study of species in which vocal development is poorly known may uncover other examples. Based on our observations of Yellow-rumped Caciques, we would expect it to occur in birds in which young males have little opportunity for social success, particularly in polygynous species. Delayed vocal maturation should be less likely in species that mate and rear young in exclusive territories, where even young birds may have a chance to breed in marginal habitat.

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